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Title: Egg predation rates and spawning success among mating territories in a lek-like mating system of *Gomphosus varius* (Pisces: Labridae)

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Terry J. Donaldson, PhD, Chairman, Thesis Committee

Spawning aggregations provide an efficient way for many fish species to attempt to maximize their reproductive success. The spawning aggregations of many species are often exploited for commercial and subsistence fisheries and are also objects of interest to the tourism industry. However, little is known about the ecological interactions of many aggregating species and the organisms that rely on their gametes for food. While a considerable number of species of wrasses and parrotfishes (family Labridae) form spawning aggregations, our knowledge of the dynamics of these events is quite variable. Through observations of spawning behavior and population density counts, this study provided insight into the workings of a spawning aggregation with a lek-like mating system of the labrid, *Gomphosus varius* at Finger Reef, Apra Harbor, Guam. Finger Reef is a popular snorkel and diving destination, and tourists often feed the fish at this location. Spawning by *G. varius* occurred daily, beginning in the late morning and ending in the early afternoon. Male spawning success was highly skewed by mating territory location with males in the outer seaward mating territories being more successful than those in the middle and inner areas of the spawning aggregation. Within the outer territories, male mating success was also skewed, with the male holding the centrally-located territory having greatest success. Gamete predation, mostly by damselfishes (Pomacentridae), occurred occasionally within this aggregation site and linearly increased with the spawning frequency of *G. varius*. The population densities of egg predators were distributed equally across the spawning aggregation site. Finally, courtship was interrupted most frequently at the inner spawning territories. These observations have heightened our knowledge of labrid reproductive behavior and provide a basis for future comparisons of spawning success, egg predation rates, and courtship interruption rates with other spawning aggregation sites.

TO THE OFFICE OF GRADUATE STUDIES

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EGG PREDATION RATES AND SPAWNING SUCCESS AMONG MATING TERRITORIES IN A LEK-LIKE MATING SYSTEM OF *GOMPHOSUS VARIUS* (PISCES: LABRIDAE)

BY

Alisha M. Gill

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Introduction

Predator-prey interactions are important in structuring biological communities. Predation can impact communities in both direct and indirect ways, affecting fishes' abundances, morphologies, and behaviors (Hixon 1991). Tropical reef fish communities are considered to be much more heavily influenced by predation pressure than other communities (Johannes 1978), and predation appears to be the largest source of mortality of tropical reef fishes (Carr and Hixon 1995). Johannes (1978) found that the predation pressures associated with tropical reef fish species have resulted in the use of reproductive strategies that greatly differ from what is observed in fish communities at higher latitudes.

Reproductive Strategies of Tropical Fishes

Tropical marine fishes display an impressive array of reproductive strategies (Thresher 1984). Eggs can be fertilized externally or internally, resulting in the release of fertilized eggs (ovipary), as is the case in many fish species, or in live birth (viviparity) which is present in a variety of families, including the labrids (Goodwin et al. 2002). Some fish species, including deep sea anglerfishes (Ceratiidae), are sexually parasitic. In this strategy, a male attaches itself permanently to the female and releases its sperm only when the female triggers it (Pietsch 2005). Other tropical marine fish, including the zebra shark, are capable of a form of asexual reproduction known as parthenogenesis. In parthenogenesis, an embryo develops from an unfertilized egg (Feldheim et al. 2010).

Most fish species are gonochoristic; where gender is fixed and individuals express either male or female reproductive structures exclusively. Other species are hermaphroditic, with both male and female reproductive structures expressed within a single individual (Sadovy and Shapiro 1987, Sadovy de Mitcheson and Liu 2008). Hermaphroditism has been confirmed in 27 fish families, most of which are tropical marine fishes (Sadovy de Mitcheson and Liu 2008). There are two types of hermaphroditism in fishes: *serial* and *sequential*. In serial hermaphroditism, an individual fish has both male and female reproductive organs simultaneously and will alternate spawning eggs and sperm with its partner. This is more common in deep sea fish but several shallow water, tropical and subtropical species of the family Serranidae are known serial hermaphrodites (Warner 1984). Sequential hermaphroditic fish begin life with the reproductive organs of one sex and are capable of changing sex later in life. Sequential hermaphrodites are born male and later change into a female (protandry), or are born female and later change into a male (protogyny) (Warner 1984). The size-advantage model, first proposed by Ghiselin (1969), best explains when a species will benefit from hermaphroditism. This model states that if the expected reproductive output differs between the sexes with size, then an individual that changes sex at the right size will have a higher reproductive output than an individual that remains solely male or female throughout its life.

Mating systems are important factors in determining whether individuals of a given species will benefit most from protandry or protogyny (Warner 1984). Protandry is the least common form of sequential hermaphroditism. According to the size-advantage model, protandry will occur when larger individuals are more successful as females and small individuals are more successful as male. This is most often seen in monogamous species, but not exclusively so. On the other hand, protogyny is expected to occur when a smaller individual is more successful as a female and a larger individual is more successful as a male. This is common in mating systems in which large males monopolize mating by defending a spawning territory, a group of females, or both (Warner 1984). Protogyny is found in many wrasse (Labridae) and parrotfish (Labridae: Scarinae) species and is associated with strong sexual selection upon males (Avise and Mank 2009, Pandian 2011).

Protogynous hermaphroditic fishes can either be *monandric* or *diandric*. In monandric species, all fish are born female and a certain percentage of these will later change into males. In diandric species, both males and females are born and later some of the females change sex to become secondary males. Primary and secondary males are sometimes monochromatic, where both male types display the same colors (Pandian 2011). Males can also be fully dichromatic, where each male type displays remarkably different color patterns compared with females or primary males. The primary males are also referred to as initial phase (IP) males (Warner et al. 1975) and the secondary males are also referred to as terminal phase (TP) males (Munday et al. 2006, Avise and Mank 2009). Sometimes, the color difference between IP males and TP males is so dramatic that they have been mistaken for different species (Roede 1972, Robertson and Hoffman 1977). Choat and Robertson (1975) suggest that dichromatism developed from high competition among males for access to females.

Sex change is often facilitated by social conditions (Avise and Mank 2009). If a secondary male is removed from a haremic mating group, the largest, most aggressive female will begin the process of sex change and take over the role as male. However, in some species the largest female will not always change sex when the opportunity arises because their reproductive success as a male is lower than continuing to reproduce as a large female (Avise and Mank 2009). Shapiro (2010) found that the removal of up to nine secondary males from a population will result in the sex change of the same number of females. Interestingly, fish may spawn in groups to help a population assess sex ratios and trigger sex change when needed (Claydon 2004).

Primary and secondary males of the same species use different mating systems and the success of each type of male depends on the population's density (Molloy et al. 2012). Secondary males may be seen in smaller spawning groups, harems, in which they defend a territory and/or females and are most successful when population densities are low (Warner et al. 1975, Avise and Mank 2009, Molloy et al. 2012). Primary males usually spawn in larger groups (spawning aggregations) and their success is expected to be highest when population densities are high. Terminal phase males often pair spawn in territories within a haremic mating system but some species may also spawn in spawning aggregations. In both systems, primary males sometimes rush into a terminal male's permanent or temporary mating territory and attempt to initiate spawning with a female by "sneaking". Other times primary males may attempt to join a terminal male and his mate in the water column as they release their gametes by "streaking" (Warner et al. 1975, Warner 1984, Domeier and Colin 1997).

Fishes that spawn in harems can either be strictly haremic or lek-like. Those that are strictly haremic are characterized by a dominant male that defends a permanent territory to which several females are attached (Colin and Bell 1991, Gladstone 1994). Mating usually occurs daily and males patrol their territories, checking on their females. On the contrary, lek-like systems are characterized by female mate choice (Trail 1985, Sherman 1999). Leks are quite rare but taxonomically abundant, occurring in insects, birds, mammals, amphibians, and fishes (Arita and Kaneshiro 1985, Sherman 1999). In these systems, males defend a temporary spawning territory devoid of valuable resources.

Leks may stand alone or be within a spawning aggregation site that females migrate to (Loiselle and Barlow 1978, Gladstone 1994, Donaldson 1995, Chop 2008). These females then choose a male to spawn with and leave after spawning (Colin and Bell 1991, Gladstone 1994, Molloy et al. 2012). However, in at least one fish species, females may spawn with one or more males repeatedly during a spawning session (Donaldson 1990). In most systems, only a few males do all of the mating leading to a highly skewed mating success (Emlen and Oring 1977a, Moyer and Yogo 1982, Arita and Kaneshiro 1985, Kirkpatrick and Ryan 1991, McDonald and Potts 1994, Petrie et al. 1999, Sherman 1999, Duraes et al. 2009).

There are three hypotheses regarding the formation of leks: the female preference hypothesis, the hotshot hypothesis, and the hotspot hypothesis (Dastagir et al. 1997, Sherman 1999, Desvignes et al. 2017). The female preference hypothesis states that males tend to aggregate because the females like to choose mates from groups where they are safer. The hotshot hypothesis states that aggregations are formed around attractive males so that lesser males can increase their chances of being noticed. Finally, the hotspot hypothesis states that aggregations form near places that females often visit. All three hypotheses have support from different taxa. However, the hotspot hypothesis is most strongly supported across the literature (Dastagir et al. 1997, Sherman 1999, Desvignes et al. 2017).

Spawning aggregations are defined by Domeier and Colin (1997) as “a group of conspecific fish gathered for the purposes of spawning, with fish densities or numbers significantly higher than those found in the area of aggregation during the non-reproductive periods.” These aggregations can contain dozens to tens of thousands of individuals (Domeier and Colin 1997, Domeier 2012, Molloy et al. 2012). The family Labridae supports a considerable number of aggregating species (Claydon 2004). Spawning aggregations are not well understood; how, why, and when they are formed can be explained by many factors. Many commercially important fish species spawn in aggregations, thus there is also an economic motivation to better understand this important phenomenon. Unfortunately, the aggregations of many commercially important species occur in areas that are difficult to reach. Studying easily-accessed spawning aggregations of model fish species that are not commercially important can help us draw conclusions about targeted species and inform management decisions (Claydon 2004, Heyman et al. 2010, Russell 2017).

All fish that spawn in aggregations often share the following characteristics: they are usually larger species that form in populations with higher densities, and all species, except for *Pseudobalistes flavimarginatus* and *Balistoides viridescens*, release pelagic eggs that are buoyant and remain in the water column until hatching (Gladstone 1994, Claydon 2004, Colin 2012c, Donaldson and Dimalanta 2012). Spawning aggregations can be divided into two groups; *transient* and *resident*. Transient spawning aggregations are typically formed by larger pelagic or reef species and may involve a long migration of days to weeks in order to reach the spawning aggregation site. Resident spawning aggregations are usually formed by smaller reef species (although some much larger species form them as well) and occur within the home ranges of the individuals involved (Domeier and Colin 1997). The ability to spawn in either of these aggregations depends upon several factors including the population density of a species and their ability to overcome migration costs (Claydon 2004, Colin 2012b, Nemeth 2012).

Spawning and Predation Risks

Spawning is a time of increased vulnerability for fish and often draws the attention of predators. The behaviors associated with spawning play important roles in the survival of a fish and their offspring (Hunter 1980). For many species, spawning is a predictable event that involves multiple individuals leaving the safety of their territories to partake in colorful or animated displays ending in the release of large amounts of eggs and sperm. Some species have even been noted as having a sort of "spawning stupor" making them more approachable than usual and during this time are especially susceptible to piscivores (Johannes 1978). Recently spawned eggs are a common food for many planktivores (Robertson and Hoffman 1977). Many observations of spawning fish have noted the presence of planktivores during spawning events, although egg predation rates may vary greatly across locations and species (Johannes 1978, Colin and Clavijo 1988, Colin and Bell 1991, Claydon 2004).

The impact that planktivores have upon a population can be direct, by influencing larval success through the consumption of eggs and sperm, or indirect, by influencing spawning behaviors of fishes (Sancho et al. 2000). The dynamic-game model shows that mate choice is not just influenced by mate density and sex ratios but is also strongly influenced by predation (Crowley et al. 1991). This model predicts that as the risk of predation increases, female fish become less selective in their mates (Forsgren 1992). As is the case in most animals, many female fish species prefer large, brightly colored males. Forsgren (1992), however, found that female sand gobies did not select these males when a predator was present. Furthermore, Moyer (1984) found that when wrasses of the species *Pteragogus flagillifer* were subjected to excessive egg predation, the spawning success of the most dominant males in a territory was altered. Also, planktivores awaiting the release of eggs sometimes get too close to spawning fish and will interrupt their courtship so spawning does not occur (Colin and Clavijo 1988).

In general, spawning for many fish is thought to occur at times and locations that reduce the chance of predation, increase chances of egg dispersal, and increase the success of larval survival and settlement (Claydon 2004). Fish eggs are an important part of diurnal planktivore diets but this is not the case for nocturnal planktivores (Hobson and Chess 1978), so many fish spawn at night or twilight to reduce the risk of egg predation. Even so, many species spawn during daylight and therefore, must rely upon other biotic or abiotic factors that discourage egg predation and promote their dispersal. For example, fish spawn in areas where eggs have the best chance of being carried away from predators (Robertson and Hoffman 1977). To increase reproductive success, spawning usually occurs in areas with optimal current, during prime tidal conditions, and at depths high enough above the substrate to prevent non-swimming predators from reaching their eggs (Thresher 1984, Claydon 2004).

There are several ways that fish can reduce the risk of gamete predation during spawning. Species that spawn pelagic eggs, including members of the Labridae, use a spawning rush that is characterized by rapid swimming towards the surface followed by the release of gametes and a quick return to the bottom (Thresher 1984, Domeier and Colin 1997). This act gives eggs enough time to achieve buoyancy so they can float away rather than drift down to benthic predators (Johannes 1978, Moyer 1987, Colin and

Clavijo 1988). In wrasses, terminal phase males sometimes chase away awaiting predators before spawning (Robertson and Hoffman 1977). Planktivores tend to prefer larger spawning aggregations over smaller spawning groups (Molloy et al. 2012), which could either be due to the conspicuousness of these larger spawning aggregations or because a larger amount of sperm and eggs are released, thus increasing the probability of a successful predation event. However, Molloy et al. (2012) argue that the benefits of spawning in large aggregations outweigh increased detection by predators.

Spawning in larger aggregations can reduce predation by planktivores via a dilution effect or via predator satiation. The dilution effect assumes that the greater the number of eggs that are present, the less chance there is of any one being consumed (Claydon 2004, Molloy et al. 2012). The predator satiation hypotheses states that predators at aggregations are presented with more food than they can eat (Johannes 1978). Interestingly, Moyer (1987) suggests that while 42.3% of observed gamete clouds were preyed upon by planktivores, this number would have been higher had spawning rushes not occurred in clusters. The planktivores at these aggregations only attacked the first few gamete clouds and ignored the rest while they ate these gametes.

***Spawning Characteristics of* Gomphosus varius**

To increase our understanding of spawning aggregations and the effect of predation by planktivorous fishes on spawned gametes, my research aimed to compare the spawning rates, courtship interruptions rates, and predation rates on the eggs of the wrasse *Gomphosus varius* between territories of a lek-like mating system within a spawning aggregation.

Gomphosus varius (Labridae) is commonly found in the tropical reefs of the Indo-West Pacific (Myers 1999). This species is diurnal and is mostly solitary but sometimes can be seen in small groups. Individuals can reach lengths of 30 cm and adults are characterized by their elongated mouths. *Gomphosus varius* is a protogynous hermaphrodite and is known to spawn in harems and spawning aggregations with or without a lek-like mating system (Colin and Bell 1991).

Few prior studies involving the reproduction and associated predation of *G. varius* have been published but Colin and Bell (1991) provide a detailed description of a lek-like haremic system of *G. varius* at Enewetak Atoll in the Marshall Islands. At this location, *G. varius* spawned 20 days out of the month and spawning events were more frequent during and leading up to a full moon. Spawning peaked at high tide and occurred all day, beginning just after sunrise and ending after sunset. Terminal phase males were territorial during reproductive hours with male-male aggression being common. Terminal phase males positioned themselves in the water above a coral head and waited for a female to approach. After a female approached, the male positioned himself above the female and fluttered his pectoral and caudal fins while changing his color to blue and intensifying the green bar on his side. The female led spawning rushes that had an apex as shallow as one meter deep. Interestingly, despite the presence of numerous pomacentrids, planktivory was not observed in any of the recorded spawning events of *G. varius.*

On Finger Reef, Apra Harbor, Guam, *G. varius* spawns daily throughout the year utilizing a lek-like mating system within a resident spawning aggregation, where males establish temporary mating territories. A territory within the lek is defined as an area that is held and protected by a male for courtship and mating (Arita and Kaneshiro 1985).

Male mating success appears to be skewed as a consequence of the location of those territories; males with territories on the seaward edge of the reef experience greater courtship success compared with males with territories found more shoreward on the reef (Donaldson unpublished data). Due to the popularity of these seaward territories, the males holding them appear to be more heavily targeted by egg predators. Five species of egg predators have been observed regularly eating spawn at both systems. These species are *Thalassoma hardwicke* (Labridae)*, Abudefduf sexfasciatus, Abudefduf vaigiensis, Chromis viridis,* and *Chromis atripectoralis* (all Pomacentridae).

Objectives

In this study, I used a combination of in-field observations and population surveys to address questions regarding the courtship success and egg predation associated with a spawning aggregation of *Gomphosus varius*. The following are compared between temporary mating territories of *G. varius:* 1) male courtship success, 2) behavioral responses to egg predation attempts, 3) egg predation rates, and 4) egg predator and *G. varius* population densities.

In lekking species, male mating success can be estimated as the number of females that he copulates with (Kodric-Brown 1977, Fiske et al. 1998). It is not uncommon for only a few of the males in a lek to do the vast majority of the spawning (Emlen and Oring 1977b, Moyer and Yogo 1982, Arita and Kaneshiro 1985, Kirkpatrick and Ryan 1991, McDonald and Potts 1994, Petrie et al. 1999, Sherman 1999, Duraes et al. 2009). Fish spawn at locations that provide their gametes with the best chance of survival (Robertson and Hoffman 1977). To increase reproductive success, spawning usually occurs in areas with optimal current, during prime tidal conditions, and at depths high enough over the substrate to prevent non-swimming predators from reaching their eggs (Claydon 2004). The outer territories at Finger Reef have these characteristics, they are deeper and closer to the mouth of the harbor than the inner and middle territories. Therefore, it is predicted that the males holding outer temporary mating territories will have higher spawning success.

Multiple studies have noted changes in courtship and spawning behavior in response to predation attempts (Warner et al. 1975, Robertson and Hoffman 1977, Colin and Bell 1991). Behavioral responses to planktivores include defensive action by a dominant male, delayed courtship, and interrupted courtship by either males or females. Some other studies, however, have reported that some spawning fish show no response to predators (Johannes 1978, Colin and Clavijo 1988). The responses of spawning fishes to planktivores appear to vary by species and location. In outer territories favored by male *G. varius,* it is predicted that males will interrupt courtship to defend their territories more than males holding middle and inner territories.

Larger spawning groups tend to be targeted more often by planktivores than smaller mating systems (Molloy et al. 2012). It is unclear if this is due to the conspicuousness of aggregations or because the large amounts of eggs increase the chance of successful egg predation. Conversely, Sancho et al. (2000) found that a planktivorous triggerfish (*Melichthys niger*) preferred feeding upon eggs of pair spawning species over aggregative spawning fish. The authors suggested, however, that this was because the species that spawned in aggregations at this location had smaller eggs. Additionally, Colin and Bell (1991) observed a lek-like harem of *G. varius* in the Marshall Islands and despite the presence of many pomacentrid planktivores, no egg predation was observed. Because males holding the few territories located on the seaward side of Finger Reef are predicted to have the greatest proportion of spawning events at this aggregation site, it is predicted that egg predation rates will be higher in outer territories of *G. varius*. Furthermore, it is also predicted that egg predator population densities will be higher in outer territories of *G. varius.*

Methods

Site Description

Apra Harbor, a deep-water commercial and naval port, is situated on the western coast of the island of Guam, Mariana Islands (Figure 1). Finger Reef lies within the harbor on the southern boundary. The depth of Finger Reef ranges from 1-6 m and the benthic composition is predominantly *Porites rus* coral. This site is frequented by recreational divers and snorkelers, and fish feeding by both has been observed here. *Gomphosus varius* courts and spawns using a lek-like mating system within a spawning aggregation that occupies about 800m^2 of this location.

Data Collection

Territories of spawning male *G. varius* were located using snorkeling and SCUBA. Transects were swam along the reef and when a courting male was observed, I marked the location with a colored-coded zip tie and photo that was tagged with a GPS point. These methods were repeated until all male mating territories within Finger Reef were marked (Figure 2). Next to ensure that behaviors of spawning fish do not change in the presence of an observer, cameras were placed near spawning males for an hour. These recorded behaviors were compared to direct observations.

Figure 1: Map of the study site, Finger Reef (highlighted in yellow), located along the southern shore of Apra Harbor, Guam, Mariana Islands. GoogleEarth Image © DigitalGlobe.

Figure 2: Map of the temporary mating territories of *Gomphosus varius* on Finger Reef, Guam. The outer mating territories are GVA, GVC, and GVF. The middle mating territories are GVG, GVE, and GVI. The inner mating territories are GVD and GVH. GoogleEarth Image © DigitalGlobe.

A total of eight active *G. varius* spawning territories were found on Finger Reef; three in the outer area, three in the middle area, and two in the inner area. All data was collected between January 2018 and May 2018. Over 36 hours of observations were conducted, and spawning occurred on 17 of 20 observation days. Each day, spawning occurred between the hours of 0900H and 1400H with the start and end time varying daily.

Each day, up to four territories were selected randomly and the behavior of the male holding the territory was observed for 30 minutes each. During these observations the following were recorded: the number of courtship attempts by each male, the number of successful spawning events, the number of interrupted courtship attempts, the gender of the individual aborting the courtship attempt, the number of egg predation events, and the species of egg predator. These methods were repeated at each mating territory four times throughout the study.

To estimate the species composition, abundance, and density of *G. varius* and the egg predators within each spawning territory, I used NOAA's Stationary Point Count (nSPC) Method (based upon Bohnsack and Bannerot 1986). Nine visual "cylinders" with a diameter of 10 meters and height of no more than 10 meters were established, with three each located within inner, middle, and outer *G. varius* mating territory zones on Finger Reef (Figure 3). Observations of egg predators and *G. varius* were conducted within each cylinder for a five-minute period to assess the species present, and then for a 10-minute period to estimate the abundance of each species. If a designated egg predator species was no longer present while I was recording abundances, I provided my best estimate of the number of fish present during my original sighting. If a species that was

Figure 3: Map of the stationary point count cylinder locations used to determine planktivore population densities on Finger Reef, Guam. Locations NSPC1, NSPC2, and NSPC3 correspond with the outer mating territories of *Gomphosus varius*. Locations NSPC4, NSPC5, and NSPC6 correspond with the middle mating territories of *G. varius*. Locations NSPC7, NPSC8, and NSPC9 correspond with the inner mating territories of *G. varius*. GoogleEarth Image © DigitalGlobe.

not originally listed and was observed at this time, I recorded its abundance anyway. Fish sizes were not recorded for this study. Surveys were replicated for a total of two times per cylinder during the course of the study.

Statistical Analysis

Successful spawns and courtship interruption count data had zero-inflated, negative binomial distributions that were tested using hurdle models. These models have two parts; the first describes the probability of a zero count and the second describes the expected rates of the non-zero counts. Tests of significance took both parts into account simultaneously. Population density data were tested for normality using a Shapiro-Wilk test. After confirming normality, a one-way analysis of variance (ANOVA) was used to test for differences in densities of planktivorous fishes between outer, middle, and inner mating territories. Predation events were rare and could not be compared between mating territory locations. Instead, a linear regression model was performed to determine the relationship between predation rates and spawning rates.

Results

Leading up to spawning, groups of males were observed swimming around together, no male on male aggression was observed during this time. Directly before spawning began, males positioned themselves above their territories that were usually located above a prominent coral head. At this time, males chased both planktivores and conspecific males from their territories. Females began migrating to the spawning site and chose a territory at which they waited to spawn. When females arrived at a male’s territory, he began courtship by swimming in circles above her and fluttering his pectoral fins (Figure 4a). Courtship was occasionally interrupted by a female that ignored the male and returned to the coral head or by the male chasing away other males and planktivores. Spawning occurred when a female swam up to meet the male. The pair then rapidly swam towards the surface with their bellies touching, released their gametes near the surface, and returned to the bottom (Figure 4b). After the release of gametes, various planktivore species sometimes rushed to the gamete cloud and consumed the gametes within it (Figure 4c). After spawning, the male continued with courtship and territory defense. All observed spawns were pair spawns between an initial phase female and terminal phase male. Only two events of sneaking by other terminal phase males were observed. There were no observations of predation attempts on spawning adults by piscivores observed at the site. Occasionally during spawning hours males appeared to "herd" females from other areas of the reef into their territories.

Spawning Rates

There was a significant difference in spawning rates between mating territory locations; 98.8% of spawning occurred in the outer territories (Figure 5) and 90.3% of all spawning occurring solely at Territory C (Figure 6). The mating territory location, however, influenced the probability of spawning occurring with the outer territories being significantly different from the inner and middle territories (z-statistics= -2.069 and -2.157 respectively, for the probability of obtaining zero counts, $P<0.05$ for both zero counts comparisons between mating territory locations). The mating territory location, however, does not predict the spawning rate. Within the outer territories, the mating territory location does not influence the probability of spawning occurring but it does predict the spawning rate with Territory C being significantly different from Territory F

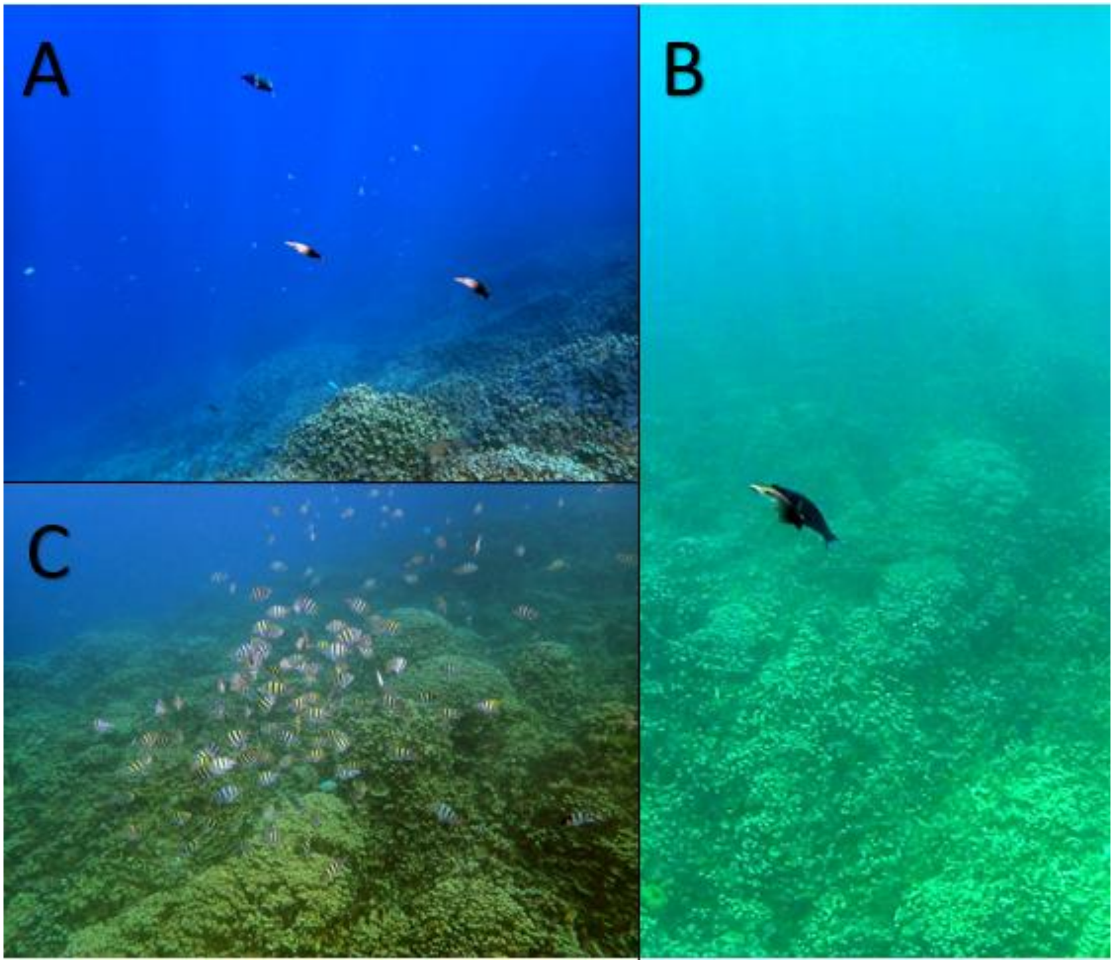

Figure 4: Photographs of the behaviors associated with spawning *Gomphosus varius*. (A) A terminal phase male *G. varius* courts two initial phase females. (B) A terminal phase male and an initial phase female *G. varius* begin a spawning rush. (C) A group of *Abudefduf sexfasciatus* and *Abudefduf vaigiensis* consume the recently spawned gametes of *G. varius*.

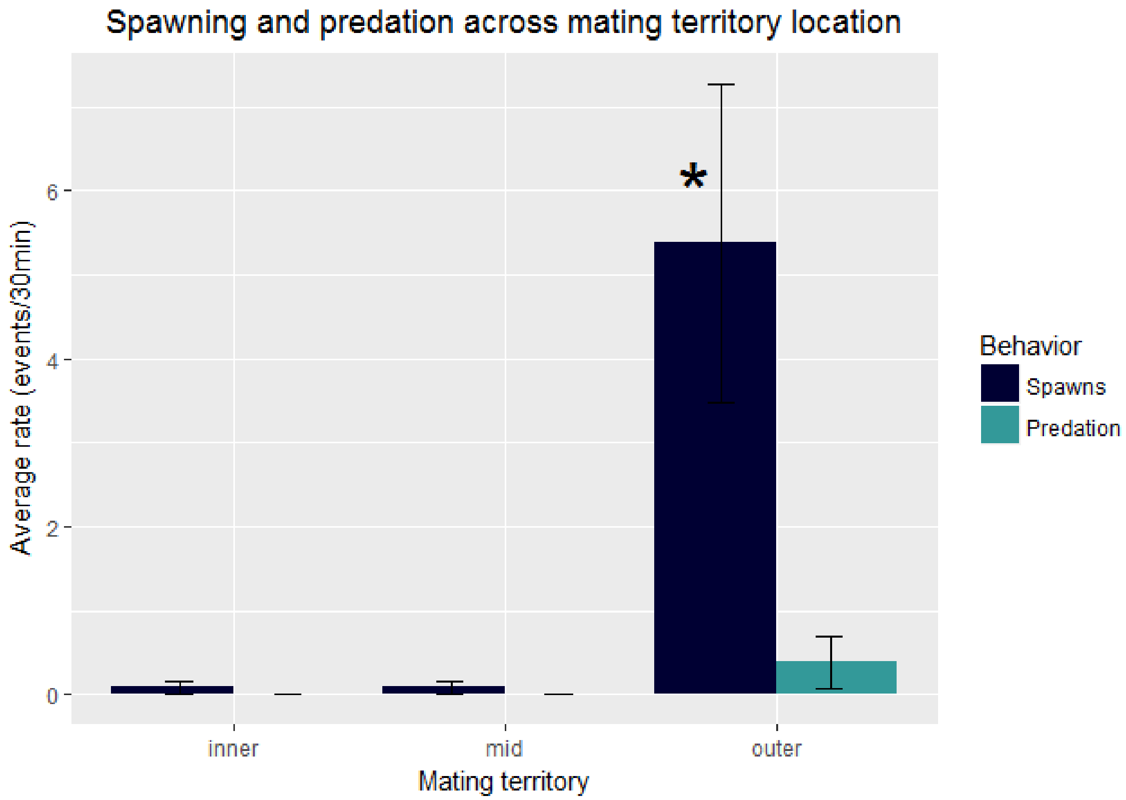

Figure 5: Spawning and predation rates across temporary mating territory locations of *Gomphosus varius*. The majority of spawning events and all predation occurred in the outer mating territories (P<0.05).

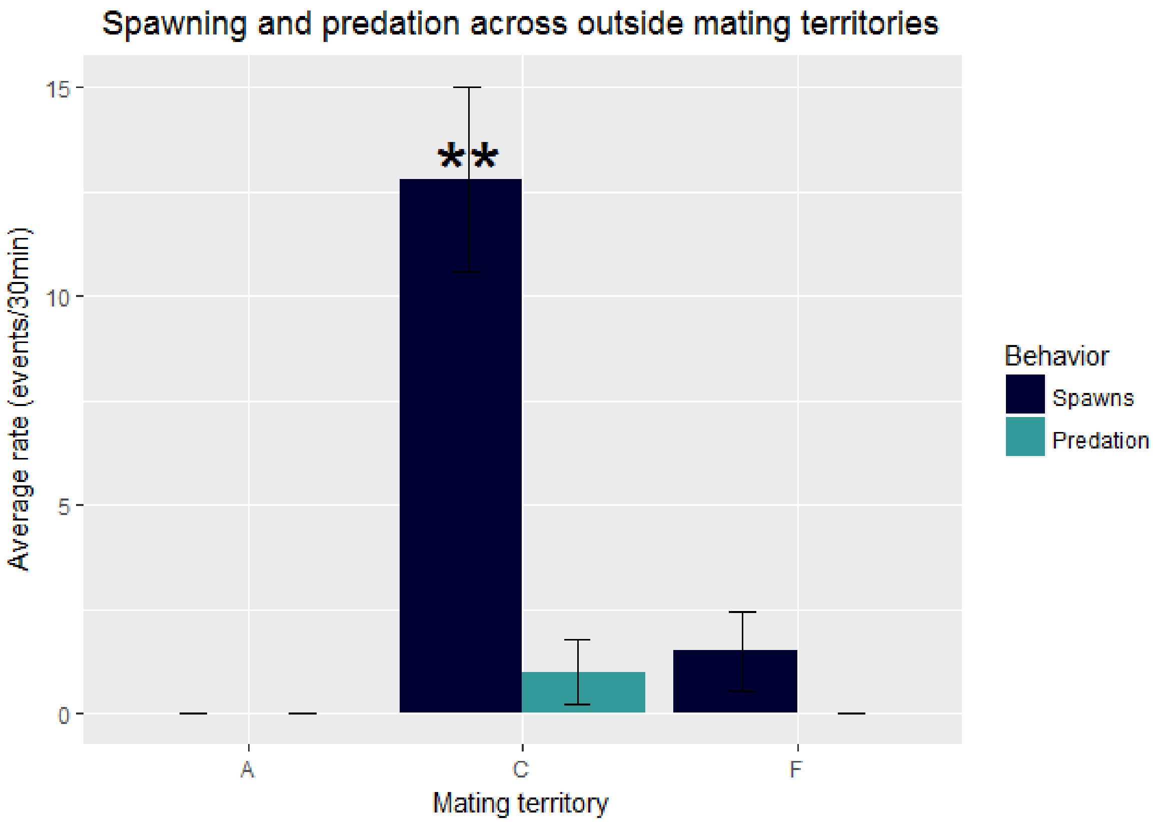

Figure 6: Spawning and predation rates across outer temporary mating territories of *Gomphosus varius*. The majority of spawning events and all of predation occurred in temporary mating territory C (P<0.01).

(z-statistic= -3.235 for the difference in spawning rates where non-zero counts existed, $P<0.01$ for zero-inflated hurdle comparisons of territories C and F).

Predation Rates

All egg predation events occurred at Territory C. Predation was minimal during the study period, however, and it occurred in only 8.2% of all spawns (Figure 5 and 6). Predation rates were positively and linearly correlated with spawning rates (Figure 7, $R^2=0.6115$, $P<0.05$).

Population Densities

There was no significant difference in the densities of planktivorous fishes across mating territory locations (Figure 8 and 9, F-statistic=0.781, $P=0.476$, one-way ANOVA).

Courtship Interruption Rates

There was a significant difference in both male and female courtship interruption rates between mating territory location (Figure 10). For females, the mating territory location does not influence the probability of female courtship abandonment occurring. However, it does predict the rate of abandonment with the inner territories being significantly different from the middle and outer territories (z-statistic= -5.007 and -4.528, respectively for the difference in spawning rates where non-zero counts existed, $P<0.001$ for both zero-inflated hurdle comparisons of mating territory locations). For males, the mating territory location influences the probability of male courtship abandonment occurring with the inner territories being significantly different from the middle (z-statistic= -2.289 for the probability of obtaining zero counts, $P<0.01$ for zero

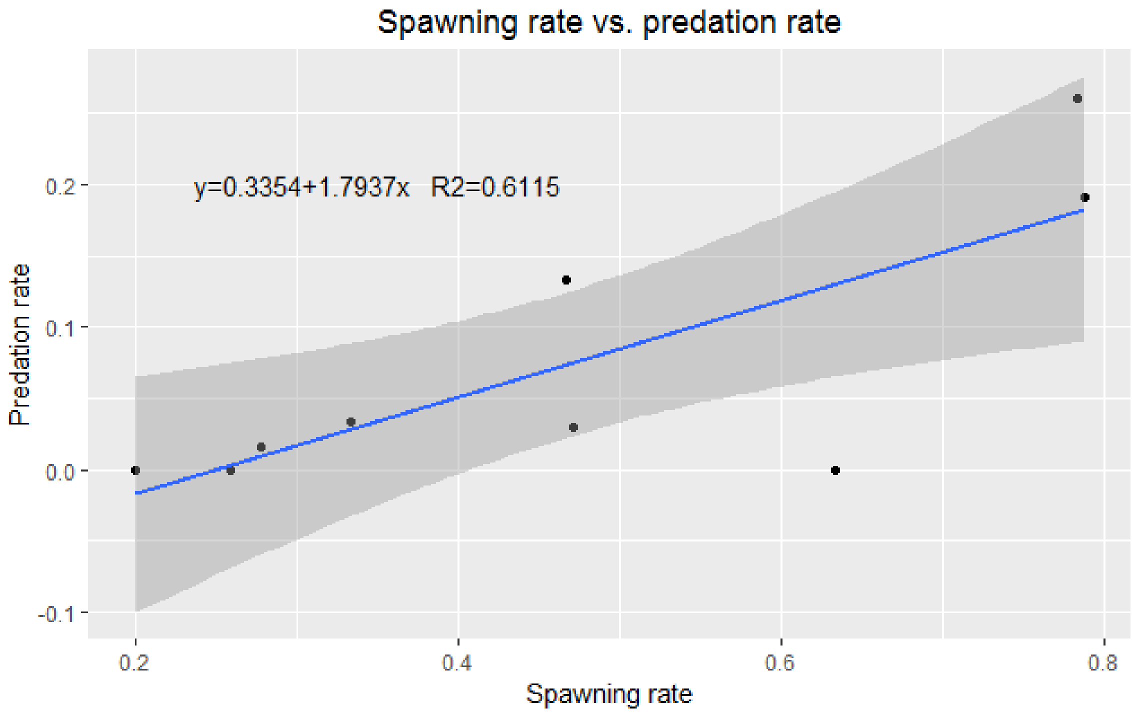

Figure 7: Linear correlation between predation rates and spawning rates of *Gomphosus varius* (P<0.05). Shaded area indicates a 95% confidence interval.

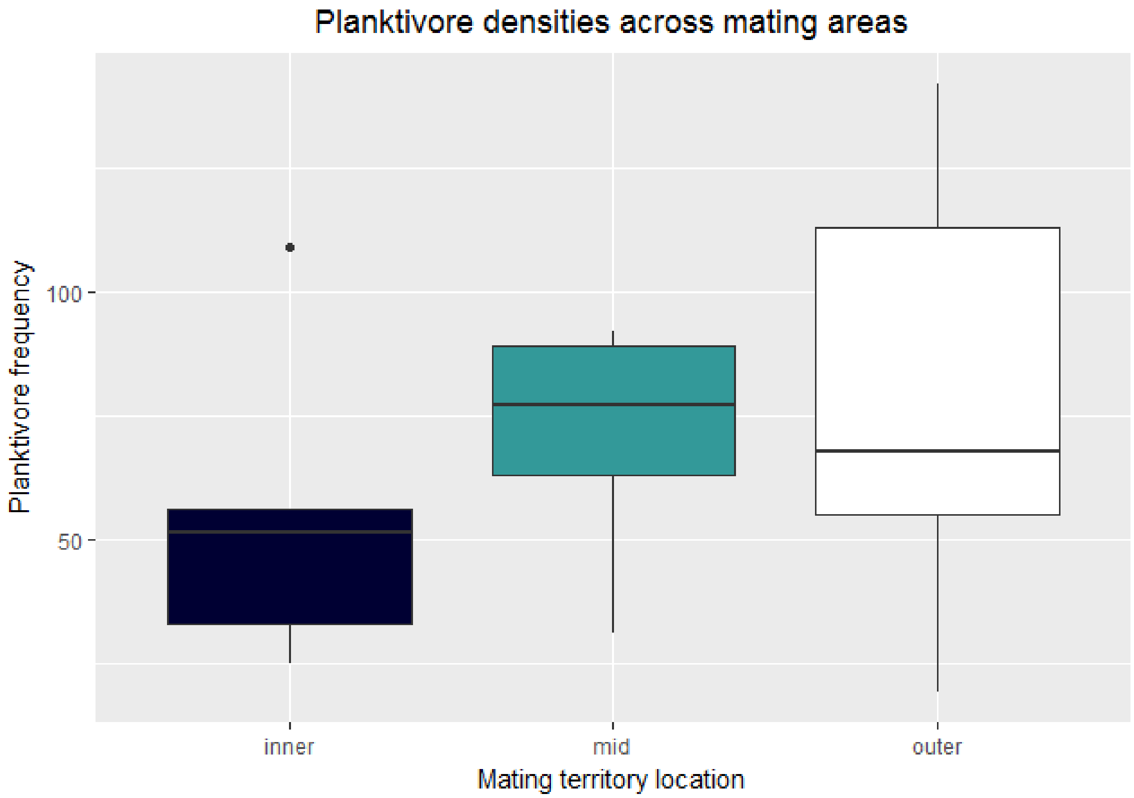

Figure 8: Population densities of planktivores across temporary mating locations of *Gomphosus varius* on Finger Reef, Guam.

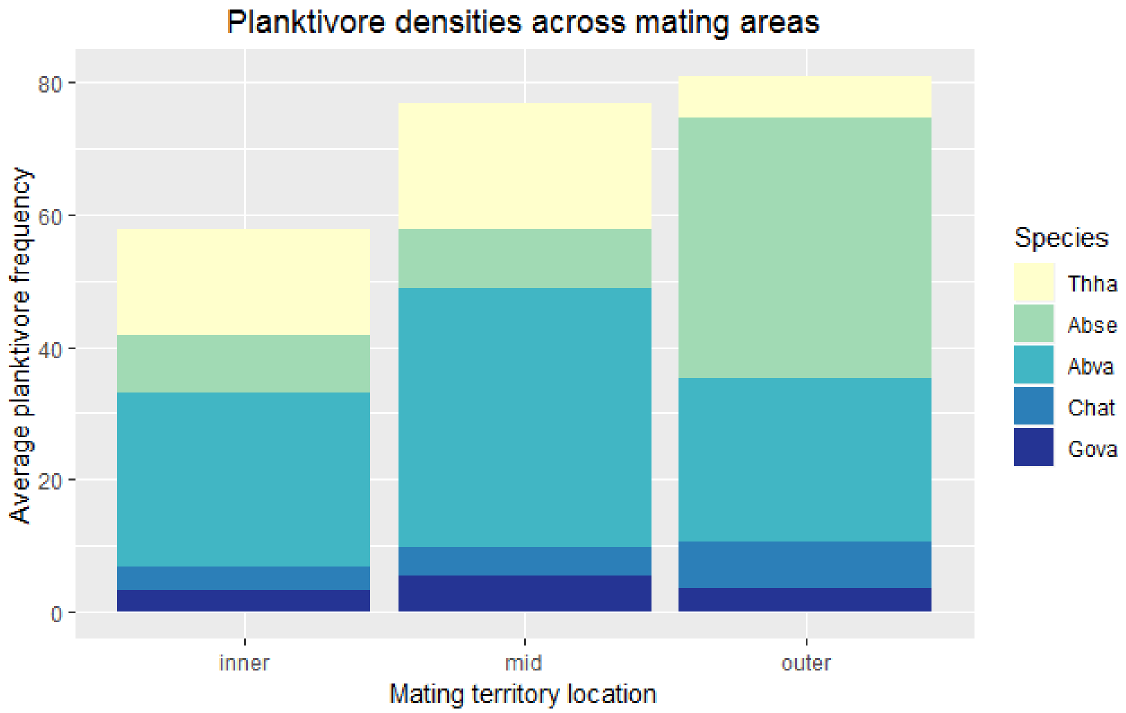

Figure 9: Species distribution of planktivores and *Gomphosus varius* across temporary mating territory locations on Finger Reef, Guam. The species observed were as follows: *Thalassoma hardwicke* (Thha), *Abudefduf sexfasciatus* (Abse), *Abudefduf vaigiensis* (Abva), *Chromis atripectoralis* (Chat), and *Gomphosus varius* (Gova).

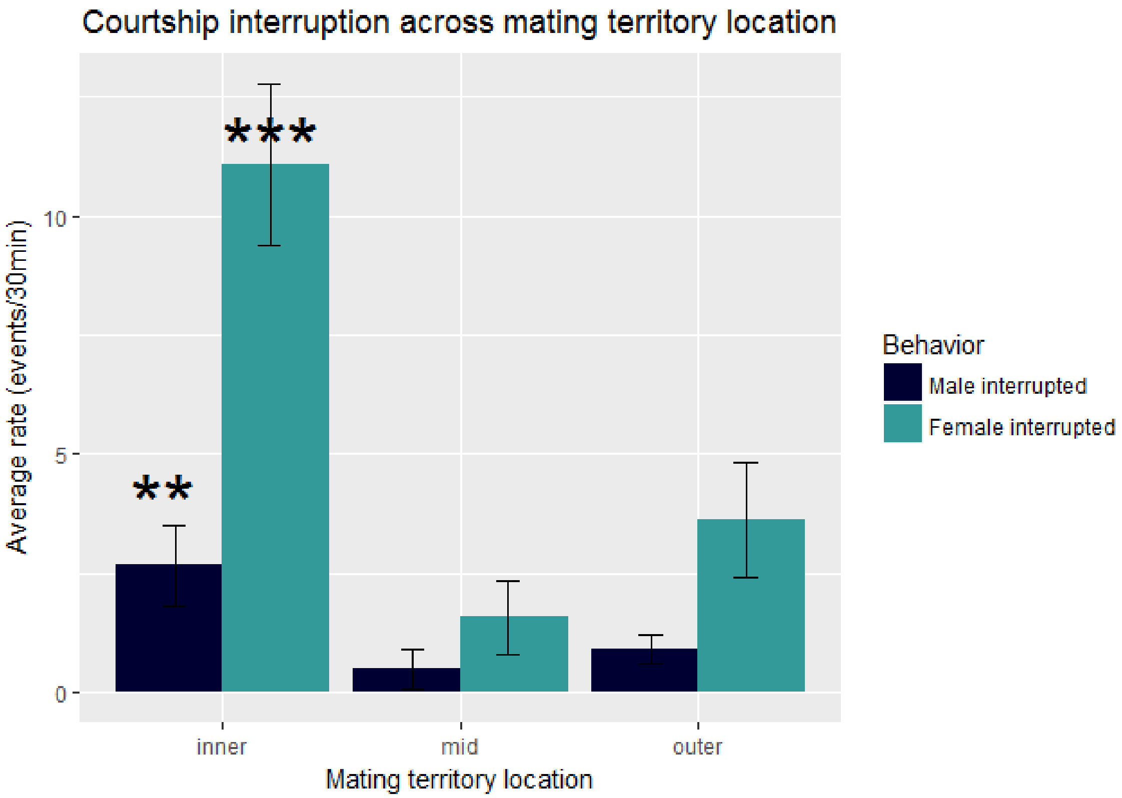

Figure 10: Male and female courtship interruption rates across temporary mating territory locations of *Gomphosus varius*. The rates of interruption in the inner territories were significantly different from the middle and outer territories for both males and females (P<0.01 and P<0.001 respectively).

counts comparisons between mating territory locations). Mating territory location, however, does not predict the rate of male courtship abandonment.

Discussion

The lek-like mating strategy used by *G. varius* at Finger Reef, Guam is not an uncommon strategy among labrids. Colin and Bell (1991) described the mating systems of various species at Enewetak Atoll in the Marshall Islands and found eight different species that utilized a lek-like mating strategy. These included *G. varius*, along with several species of *Thalassoma* and *Scarus*. Additionally, Desvignes et al. (2017) found that *Gomphosus caeruleus* at Reunion Island in the Indian Ocean spawns in a lek-like system. The courtship and spawning behaviors of *G. varius* at Finger Reef and Enewetak Atoll, and of *G. caeruleus* at Reunion Island are nearly identical. Both *G. varius* at Finger Reef and *G. caeruleus* spawned daily from late morning to early afternoon. *Gomphosus varius* at Enewetak Atoll, on the other hand, was observed spawning from sunrise to sunset. While peak spawning was not determined in this study, peak spawning for *G. varius* at Enewetak Atoll and *G. caeruleus* was found to be around the full moon. It is likely that this is the same for *G. varius* at Finger Reef, however, more data should be collected to confirm this.

Only pair spawning between a terminal phase male and an initial phase female was observed in all three of these studies. No instances of mating between two IP individuals was seen, however, this does not necessarily mean that *G. varius* is monandric. It is possible that initial phase males are group spawning in other locations. Colin and Bell (1991) provided anecdotal evidence of this. Histologic techniques need to be used to determine whether the species is monandric or diandric.

Males that were positioned in the more successful outer territories remained there for the entirety of spawning, but males positioned in the inner and middle territories did not remain at a single territory. Fiske et al. (1998) found that territory attendance was most highly correlated with male mating success. It is possible that females use attendance as a signal when choosing a mate. These males usually followed females that happened to be passing through which often resulted in several males trying to court a single female and thus, male-male aggression. During several observation periods, females observed waiting at inner or middle territories left due to the absence of males. The males holding territories in these areas were most likely younger and less experienced than those holding outer territories. Unfortunately, age determination using standard methods for reef fishes is destructive and therefore not possible in this study.

Spawning Rates

Males in the outer territories were predicted to have higher spawning rates and my results support this. I was, however, quite surprised at how dramatically skewed spawning success was across territory locations. Only one spawning event was seen in the middle and inner territories each. The days in which these spawns were observed were particularly busy spawning days for *G. varius*, as well as many other species that spawn at Finger Reef. It is possible that females become less selective in their mates when numbers of spawning individuals are high, and the wait time increases for spawning with a more desirable male. More data needs to be collected to find a peak spawning time and to determine if there is a correlation between it and the spawning rates found in the middle and inner mating territories.

Nearly all of the spawning was done by a single male, which is not uncommon in lekking species across all taxa (Emlen and Oring 1977b, Moyer and Yogo 1982, Arita and Kaneshiro 1985, Kirkpatrick and Ryan 1991, McDonald and Potts 1994, Petrie et al. 1999, Sherman 1999, Duraes et al. 2009). The reason for this highly skewed success is not well understood but it has been hypothesized that males in a lek are kin or that there is a hierarchal system in leks (Sherman 1999). Wiley (1973) found that peacocks lek with kin and the closer two males are positioned within the lek is correlated with how closely related they are. At Finger Reef, territory possession appeared to change throughout the course of the study. It would be useful to track territory possession and to collect genetic data to determine whether there is a hierarchy in place or if lekking males are kin. The presence of a hierarchy system at the spawning aggregation site is likely. Males were often observed swimming side-by-side in small groups, often speedily, and chasing was observed as well. Males may be using this behavior to size each other up and determining territory ownership for the day. Also, as stated earlier, males holding the middle and inner territories appeared to be younger and less experienced, further supporting this hypothesis. Hierarchal mating systems are seen in several bird species, such as the sage grouse (Arita and Kaneshiro 1985). Regardless, a male has a higher probability of mating when it is part of a lek because group displays tend to attract more females (Petrie et al. 1999).

Another interesting question is what makes these outer territories so desirable? Fish spawn at sites that have characteristics that increase the probability of gamete survival (Robertson and Hoffman 1977). To increase reproductive success, spawning usually occurs in areas with optimal current, during prime tidal conditions, and at depths high enough over the substrate to prevent non-swimming predators from reaching their eggs (Claydon 2004). The outer territories at Finger Reef appear to have these characteristics. It is unclear whether the males change territories frequently, however, I was able to identify a single individual that had a scar on his side who changed territories at least twice during the course of my study. It is probable that a physical parameter rather than the male himself is driving female preference. While the spawning aggregation site is composed of predominantly *Porites rus*, there is variation in the height and structure of coral heads (Burdick 2006). So, this is perhaps not the main factor driving site selection. It is likely that current and depth are correlated with the skewed success of mating territory location. Physical parameters of the spawning aggregation site should be collected to determine how the areas differ.

Within the outer territories there is also highly skewed reproductive success for the males holding these territories. The male holding Territory A was not observed spawning once and the male holding Territory C spawned significantly more than the male at Territory F did. So, what is driving the skewed success between the three outer territories? The physical parameters between Territories F, C, and A are most likely very similar since these territories are located so close together. Physical data, however, should be collected to confirm this. Most successful males have often been found to be positioned in the center of leks (Fiske et al. 1998) and Territory C is positioned between A and F. This central position may offer extra protection for the spawning individuals and their gametes, thus making it a more desirable spawning location. Territory C, however, was the only one that experienced gamete predation, so this might not be the case.

Predation Rates

Predation rates were predicted to be higher in the outer territories and while predation was rare, this prediction appears to be supported. Since nearly all of the spawning occurred in the outer territories, it makes sense that every predation event also occurred here. Interestingly, all gamete predation events occurred at Territory C. While the male holding Territory C did most of the spawning, the male at Territory F also had a fair amount. The male holding territory C may have drawn more attention from egg predators because of the high frequency of spawning there when compared to that in territory F. Additionally, predation rates were found to increase as spawning rates increased. This outcome is likely given that spawning events are quite obvious, and they quickly draw the attention of planktivores. Therefore, when spawning occurs frequently, the probability of egg predators encountering eggs may be higher. Spawning is known to draw the attention of predators and many observations of spawning fish have noted the presence of planktivores; however, egg predation rates greatly vary across locations and species (Johannes 1978, Colin and Clavijo 1988, Colin and Bell 1991, Claydon 2004). Interestingly, Colin and Bell (1991) didn’t observe predation on *G. varius* gametes. So, why does predation occur only in some systems or locations? Could fish feeding by tourists, which attracts various species of fishes, including planktivores, be related to this?

Finger Reef is visited by snorkelers and divers almost daily, and many of the groups that visit this reef feed the fish here. Thus, the planktivore populations are relatively high; it would be interesting to see if gamete predation differs in systems where fish feeding does not occur. Appendix A provides a map of Guam showing the locations that *G. varius* was found during NOAA surveys in 2014 and 2017. Locations that *G. varius* was observed along with species that have been observed consuming *G. varius* gametes at Finger Reef are also provided. It is likely that *G. varius* has resident spawning aggregations at one or more of these locations. It would be useful to determine which of these sites host *G. varius* spawning aggregations and compare egg predation rates between locations where fish feeding does and does not occur. Additionally, predation rates haven't been compared between large and small spawning groups, but this could be useful to determine whether spawning in larger groups reduces the relative risk of gamete predation.

During most observation periods, planktivores at the spawning aggregation site showed very little interest in spawning *G. varius*. On most days, group spawning by *T. hardwicke* took place around the same time as that of *G. varius*. The planktivores in the area appeared much more interested in the *T. hardwicke* group spawning than in pair spawning by terminal phase males and initial phase females that also occurred here. This preference for group spawning over pair spawning by planktivores was also observed by Molloy et al. (2012). A study comparing predation rates on *G. varius* spawns between days where *T. hardwicke* group spawning occurs and days it does not would be interesting, as it appears that predation on *G. varius* spawn is much higher when *T. hardwicke* is not spawning.

Interestingly, the majority of gamete predation events were by a single terminal phase *Thalassoma hardwicke*. This male had a mating territory in the same location as territory C and usually was already in the area which made it easy to feed upon eggs intermittently. There was only one instance where a group of *Abudefduf sexfasciatus* and

A. vaigiensis swarmed the recently spawned gametes of *G. varius*. As stated earlier, these species were more interested in consuming the gametes of *T. hardwicke* group spawns. Gamete predation by *Chromis viridis* and *C. atripectoralis* were not observed over the course of this study, however, previous work has shown these two species consume *G. varius* gametes.

Population Densities

Planktivore densities were predicted to be highest in the outer territories and that would correspond with higher spawning and predation rates. While the outer territories did have higher numbers of planktivores, the difference was not significant. This is most likely due to the amount of group spawning by other species that occurs closer to the middle territories of *G. varius.* The majority of planktivores on Finger Reef were the damselfishes *A. sexfasciatus* and *A. vaigiensis* and these species were often seen consuming the gametes from group spawning *T. hardwicke. Thalassoma hardwicke* also had high densities at Finger Reef, which is most likely because they also have a spawning aggregation at this site. A comparison of planktivore densities across various spawning aggregation sites of *G. varius* would be interesting to see if this pattern is common.

Courtship Interruption Rates

Outer spawning territories were predicted to experience higher courtship interruption rates that correspond with predation rates and increased male-male competition. Spawning draws the attention of predators and the behaviors associated with courtship and spawning play important roles in the survival of fish and their offspring. The impact that planktivores can have upon a population can be direct, by influencing larval success through the consumption of eggs and sperm, or indirect, by influencing spawning behaviors of fishes (Sancho et al. 2000). Sometimes, infringing egg predators interrupt courtship so spawning does not occur (Colin and Clavijo 1988). This was not the case at Finger Reef, however, and courting pairs of *G. varius* in the less successful inner spawning territories actually had much higher interruption rates.

Due to the higher densities of males in the middle and inner spawning areas, there was more male-male aggression in competition for females and territories. As stated earlier, sometimes multiple males would try to court a single female and this often lead to altercation between rival males that interrupted courtship. On the other hand, when a single male attempted to court a female, he was usually ignored by both rival males and the female who continued on her way to the outer reef spawning territories.

The females that frequent this spawning aggregation appear to spend their non-spawning time inshore towards the reef crest. Resident spawning aggregations occur within the home ranges of the individuals involved (Domeier and Colin 1997) and females were seen migrating daily through the inner and middle territories to reach the outer territories. This aggregation most likely formed here because of certain physical characteristics that drew female attention. This supports the hotspot hypothesis which states that aggregations form in areas where females are often found. Females could be attracted to this location for several reasons including foraging opportunities, however, this site likely has physical characteristics that promote egg and larval dispersal. Desvignes et al. (2017) found evidence to support this hypothesis in the lek-like mating system of *Gomphosus caeruleus* at Reunion Island in the Indian Ocean. By setting up a spawning aggregation here, even the lesser males are able to increase their chances of mating.

Courtship interruptions by both females and males in the outer territories appeared to be more often associated with encroaching planktivores rather than due to conspecifics. It is often difficult, however, to discern the reason for courtship interruption and more data should be collected to confirm this. Since the courtship interruption rates were much lower in the outer territories, egg predation most likely does not impact mate choice in this system.

Conclusion

Spawning aggregations provide an efficient way for fishes to increase their reproductive success. They are also an important resource for commercial fisheries as well as tourism. Little is known about the characteristics and dynamics of the spawning aggregating of many species, thus making it important that we increase our understanding of these reproductive systems. The family Labridae has a considerable number of species that form resident spawning aggregations, some of which utilize a lek-like mating system within an aggregation. This study provides insight into the workings of a spawning aggregation with a lek-like mating system of the labrid, *G. varius* at Finger Reef, Guam. *Gomphosus. varius* is a great model species to further our understanding of labrid reproductive behavior.

Spawning by *G. varius* occurs daily, beginning in the late morning and ending in the early afternoon. Male spawning success is highly skewed by territory location with the outer territories being more successful than those in the middle and inner areas. Within the outer territories, male mating success is also skewed, with the male holding the central territory (C) having the greatest success. Gamete predation occasionally occurs within this aggregation and is positively and linearly related to spawning frequency. The population densities of egg predators are distributed equally across the spawning aggregation site. Finally, courtship interruptions occur most frequently within the inner spawning territories. Additional data should be collected to determine peak spawning at this location as well as to determine whether there is a lunar or tidal element to predict these events. A comparison of predation rates between the outer territories may also be useful in future studies. Additionally, a study that compares gamete predation rates between sites where fish feeding does and does not occur would be useful to determine if this practice has negative impacts upon spawning aggregations.

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Appendix

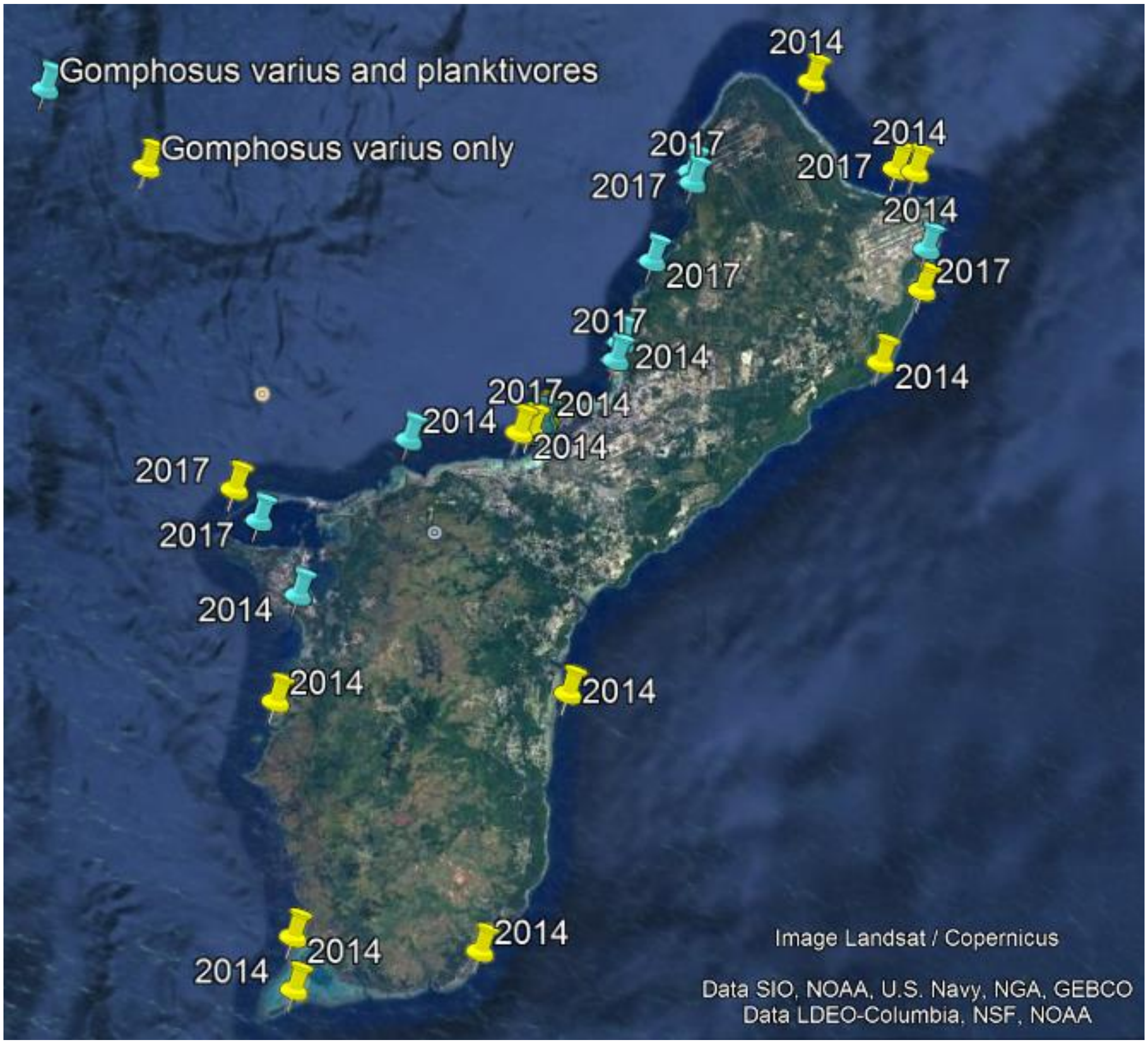

Figure 11: Map of Guam showing NOAA population survey locations where *Gomphosus varius* were found alone (yellow) and where they were found along with egg predators (blue). Surveys were completed in 2014 and 2017 (Heenan et al. 2017). GoogleEarth Image © DigitalGlobe.